Susceptibility of Upland Cotton Cultivars to *Bemisia tabaci* Biotype B (Homoptera: Aleyrodidae) in Relation to Leaf Age and Trichome Density

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ABSTRACT The relationships between leaf trichome densities, leaf age, and sweetpotato whitefly, *Bemisia tabaci* (Gennadius) biotype B, infestations of 13 upland cotton, *Gossypium hirsutum* L., cultivars were investigated in 1990 and 2000. Stoneville 474 supported higher numbers of *B. tabaci* biotype B eggs, nymphs and adults, and also had higher numbers of stellate trichomes on abaxial leaf surfaces compared with other cotton cultivars. Siokra L-23, in general, had fewer stellate trichomes and also fewer whiteflies. However, the positive trichome–whitefly density relationships were affected by the ages of leaves from different main stem cotton nodes. The youngest leaves on main stem node 1 below the terminal for all cultivars had higher numbers of stellate trichomes but fewer whiteflies compared with older leaves.

KEY WORDS *Bemisia tabaci* biotype B, *Bemisia argentifolii*, leaf age, stellate trichome, capitate trichome, small veins

Bemisia tabaci (GENNADIUS) biotype B, also called *B. agentifolii* Bellows & Perring, has been an economic pest in upland cotton, *Gossypium hirsutum* L., in the southwestern United States since 1991 (Natwick et al. 1995). Losses occur due to reduced yields and lint contamination with honeydew excreted by adults and nymphs. The development of cotton plants resistant to *B. tabaci* biotype B remains a high priority. Our previous studies (Chu et al. 1998, 1999) to identify cotton plant characteristics related to *B. tabaci* colonization agreed with others that hairy leaf cotton cultivars harbor higher populations compared with smooth leaf (with few trichomes) cultivars (Butler and Henneberry 1984, Flint and Parks 1990, Norman and Sparks 1997). These results appear valid except for extremely high trichome densities. (Butler et al. 1991) reported that adult *B. tabaci* density decreased at trichome densities of 467–847 per cm^2 of leaf area. Also, Mound (1965) did not find adult whiteflies or their eggs on the first top two leaves of some exceptionally hairy cotton plants. These results suggest a more complex explanation for *B. tabaci*-hairy leaf cotton preference than previously considered. More recently, we reported that other factors, including leaf color, morphology and leaf age related lysigenous glands, in addition to leaf trichomes, may affect *B. tabaci* biotype B oviposition and nymph densities (Chu et al. 2000a, 2000b). This report presents new information further defining the influence of leaf age on cotton leaf trichome density - *B. tabaci* relationships in thirteen upland cotton cultivars studied.

Materials and Methods

Field Studies. The studies were conducted in 1999 and 2000 at the University of Arizona's Maricopa Agricultural Research Center in randomized complete block designs with four replicates. Each plot was eight rows wide and 12.2 m long with rows spaced 1 m apart. There were two unplanted rows between plots and 3 m wide alleys between blocks. In 1999, treatments were normal-leaf cotton cultivars Deltapine [DPL] numbers 20B, 50B, 90B, NuCOTN 33B [Nu 33B], and Stoneville [ST] 474, and okra-leaf cultivars Fiber Max [FM] numbers 819 and 832, Siokra L-23, Siokra I-4/649, and 89013–114. In 2000, the five okra-leaf cultivars were replaced by four cultivars, E0223, E0798, E1028, and Siokra L-23. All cultivars were smooth leaf cottons except for the hairy-leaf ST 474. Smooth leaf cottons may have a few branched and elongate single celled stellate trichomes. All seeds were obtained commercially and treated with an insecticide - fungicide mixture. Seeds were planted on 19 and 13 April for 1999 and 2000, respectively. Plants emerged about 2 wk later and were watered at 10- to 20-d intervals during their growing seasons. Plots were not treated with any pesticides except diflubenzuron for the control of salt

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marsh caterpillars, *Estigmene acrea* Drury, on 13 August in 1999.

B. tabaci biotype B population densities were determined by picking leaves at 7 d intervals from 21 July to 6 October in 1999 and 10 July to 5 September in 2000. On each sampling date, three plants each plot were randomly selected. Leaves were picked from the main stem nodes numbers 1, 3, 5, 7, 10, and 15 in 1999 and from nodes 1 to 5 and 7 in 2000. Nodes were numbered beginning with the first expanded leaf below the plant main terminal. Leaves from node 1 measured ≥2.5 cm between the two largest leaf lobes. Nodes 15 were those in the lowest position on the main stems. A 2-cm^2 leaf disk was taken from the leaf area next to the center primary vein (Naranjo and Flint 1994). Numbers of eggs and nymphs were counted on abaxial leaf surfaces with the aid of a stereoscope. Adults per leaf were counted on three-fifth main stem node leaves in each plot in 1999 and on three leaves from each of the six main stem nodes sampled in each plot in 2000 (Naranjo and Flint 1995) on each sampling date. Stellate trichomes on abaxial leaf surfaces were counted on leaf disks from three leaves from each leaf node, except for 15, in each plot on 23 June in 1999. In 2000, stellate trichomes were counted on each sampled leaf on each sampling date. Following Radford et al. (1974) we classified cotton leaf vein sizes as large veins that include primary and secondary veins, and small veins that include tertiary and quarternary veins. Primary veins were the five veins (on a normal-leaf shaped cotton plant) that extended from the leaf base and the petiole juncture to the leaf edges. Veins branching from primary veins were classified as secondary veins, and similarly tertiary, quarternary, and quinternary veins branched from secondary, tertiary, and quarternary veins, respectively. Quinternary and lower order veins surrounded the leaf areole areas (Fig. 1). Veinlets (=vein-endings) are found within areole areas (Fig. 2). Under special lighting conditions, quarternary veins can be identified with the aid of a stereoscope, but the quinternary veins, smaller veins and vein endings do not have associated epidermal characteristics and cannot be distinguished in uncleared leaves. Two, 2 cm^2 leaf disks were punched from the base of each leaf encompassed large and small veins in 1990 and encompassed only small veins in 2000. Leaf disks from leaf 1 ranged from 0.3 to 0.6 cm^2 in areas because the small leaf size.

Laboratory Studies. Studies were designed to define the differences in leaf morphology and whitefly densities between Nu 33B and ST 474, smooth and hairy leaf cottons (Fig. 3A and 3B), respectively. Leaves from main stem nodes 1, 2, 3, 4, 5, 7, 10, and 15 were collected on 27 September from plants randomly selected in each of the four replicated plots. Petioles of picked leaves were placed in water-filled, plastic floral tubes packed with blue ice and shipped overnight to the North Dakota State University Electron Microscopy Center, Fargo, ND.

Whole leaves were traced on paper and leaf areas calculated. A 4.5-cm^2 leaf disk was punched from the area of each leaf described earlier. Each leaf disk was cut in half. One half of the disk from each leaf was held for back up. The other half was further sub-divided into samples 3–4 mm wide. All leaf sections were then fixed in 2.5% glutaraldehyde in Millonig's phosphate buffer (pH 7.4) for 3 h at 23°C. The samples were washed twice with buffer and then postfixed in buffered 2% osmium tetraoxide at 4°C. Following fixation, samples were buffer washed, rinsed in water, and then dehydrated with DMP (2,2-dimethoxypropane). After rinsing twice in absolute ethanol, the samples were critical point dried in a Tousimis autosamdri 810 critical point dryer using CO_2 as the transitional fluid. Numbers of stellate and capitate (glandular) trichomes as well as egg and nymph densities were counted using a scanning electron microscope (SEM) for 37-mm^2 leaf areas of each of the four leaves from the eight nodes of each plant.

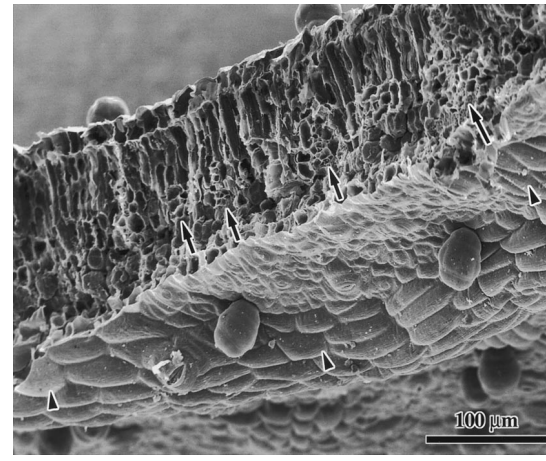

Fig. 1. A fractured cross section of cotton leaf. Arrowheads delineate an areole area on abaxial surface; the large arrow identifies a cross section of the vein limiting the areole; and small arrows identify small veins with no distinguishable epidermal characteristics. Small veins are probably used for *Bemisia tabaci* biotype B feeding.

Greenhouse Studies. Field grown cotton plants constantly add new leaves during the growing season. This

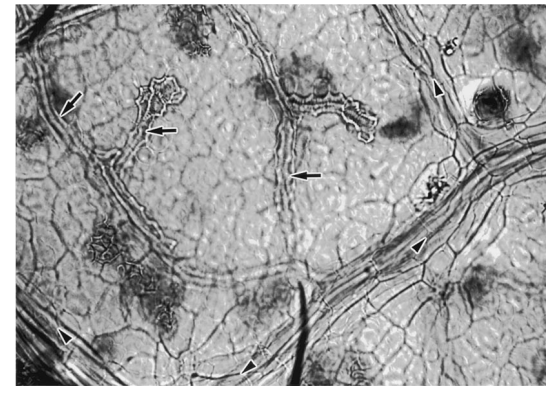

Fig. 2. A cleared leaf viewed from the abaxial leaf surface. Arrowheads delineate an areole area; arrows identify small veins or vein-lets with no distinguishable epidermal characteristics.

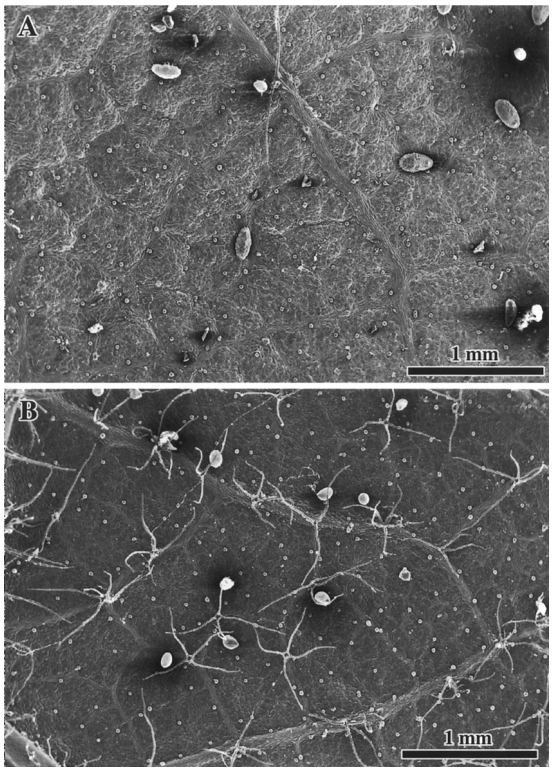

Fig. 3. Abaxial cotton leaf surfaces. (A) smooth leaf NuCOTN 33B and (B) hairy leaf Stoneville 474.

compromises some types of *B. tabaci* density sampling. For example, when the youngest leaves at node 1 down from the terminal have been exposed to *B. tabaci* infestations for 1 wk, leaves at node 2 may have been exposed for 2 wk and so on for older leaves. This study was designed to eliminate the time of exposure as a factor confounding *B. tabaci* density comparisons on leaves from different main stem nodes. Ten plants each of Nu 33B and ST 474 cultivars in the 8-leaf stage of plant development were placed individually in clear plastic cylinders (32 cm diameter by 60 cm high). Cylinder tops were covered with +300-mesh cloth for ventilation. A hole (15 cm diameter) was cut in the side of each cylinder and fitted with an open-ended cloth sleeve. Three hundred adult *B. tabaci* were released into each cage. Adults were allowed to oviposit for 2 d, and numbers of eggs were counted on one-half of each of the leaves except for those from node 1. Due to the small leaf sizes from node 1, eggs were counted on whole leaves. Numbers of stellate trichomes on small veins and between veins in areoles were counted from each leaf on three 0.65 -m^2 leaf disks punched from the leaf area described earlier. The leaf areas were measured, using video camera system (Cannon RE-650 Video Visualizer, CID, Vancouver, WA). Photosynthetic photo flux density was 600 μmole/s/m^2 (maximum), and ambient temperature and relative humidity in the cylinders ranged from 22.9 to 33.4°C and from 35 to 74%, respectively.

Data Analyses. For field studies as well as greenhouse and laboratory studies, *B. tabaci*, stellate trichome and leaf area counts were transformed using square root (x + 1) when necessary to correct for heterogeneity and calculated seasonal means were analyzed using analysis of variance (ANOVA) (Anonymous 1989) for randomized complete block designs. Mean comparisons between treatment data were either plotted or tabulated following statistical analyses. Means in all cases were separated with Student-Neuman-Keul's multiple range test at P = 0.05.

Results

Field Studies. Mean numbers of adults were significantly greater on ST 474 compared with other cultivars both in 1999 and 2000 (Fig. 4A and B). In 1999, the seasonal average of adults for ST 474 was the highest (34.3 adults per leaf), followed by the four Deltapine cultivars and five Australian cultivars (Fig. 4A). Siokra L-23 had the lowest number of adults (9.5 per leaf). In 2000, the seasonal average of adults for ST 474 was also the highest (12.9 per leaf) compared with the four Deltapine cultivars and the four Australian cultivars (Fig. 4B). Siokra L-23 and E1028 had the least (2.8 and 1.5 adults per leaf).

Mean numbers of eggs were significantly greater on ST 474 compared with other cultivars both in 1999 and 2000 (Fig. 4C and 4D). In 1999, the seasonal average of eggs for ST 474 was highest (50.3 eggs/cm^2 leaf disk), followed by DPL 50B and FX 819 (Fig. 4C). Deltapine 90B had the lowest seasonal average of eggs (19.9 eggs/cm^2 leaf disk). Similar numbers of eggs were found on leaf disks of other six cultivars. In 2000, the seasonal average of eggs for ST 474 was the highest (36.0 eggs/cm^2 leaf disk), followed by DPL 50B and NuCOTN 33B (Fig. 4D). E1028 had the lowest seasonal average of eggs (2.3 eggs/cm^2 leaf disk). Similar numbers of eggs were found on leaf disks of other five cultivars.

Mean numbers of nymphs were significantly greater on ST 474 compared with other cultivars both in 1999 and 2000 (Fig. 4E and F). In 1999, the seasonal average of nymphs for ST 474 was the highest (24.7 nymphs/cm^2 leaf disk), followed by DPL 50B, FX 819 and 89013–114 (Fig. 4E). Siokra I-4 and FX 832 had the least numbers of nymphs (8.0 and 7.0 nymphs/cm^2 leaf disks). Similar numbers of nymphs were found on four other cultivars. In 2000, the seasonal average of nymphs for ST 474 was the highest (13.3 nymphs/cm^2 leaf disk), followed by DPL 50B (Fig. 4F). The seasonal average of nymphs for E1028 was the least (0.6 nymphs/cm^2 leaf disk). Similar numbers of nymphs were found on other six cultivars.

For all 10 cultivars studied in 1999, the highest seasonal average numbers for eggs occurred on leaves from nodes 3 and for nymphs from nodes 5 (80.9 eggs and 25.6 nymphs/cm^2 leaf disk) compared with other nodes (Table 1). The seasonal average numbers of stellate trichomes (on all veins and between veins) for all 10 cultivars was the highest on leaves from node 1 (199.0 trichomes/cm^2 leaf disk) compared with those

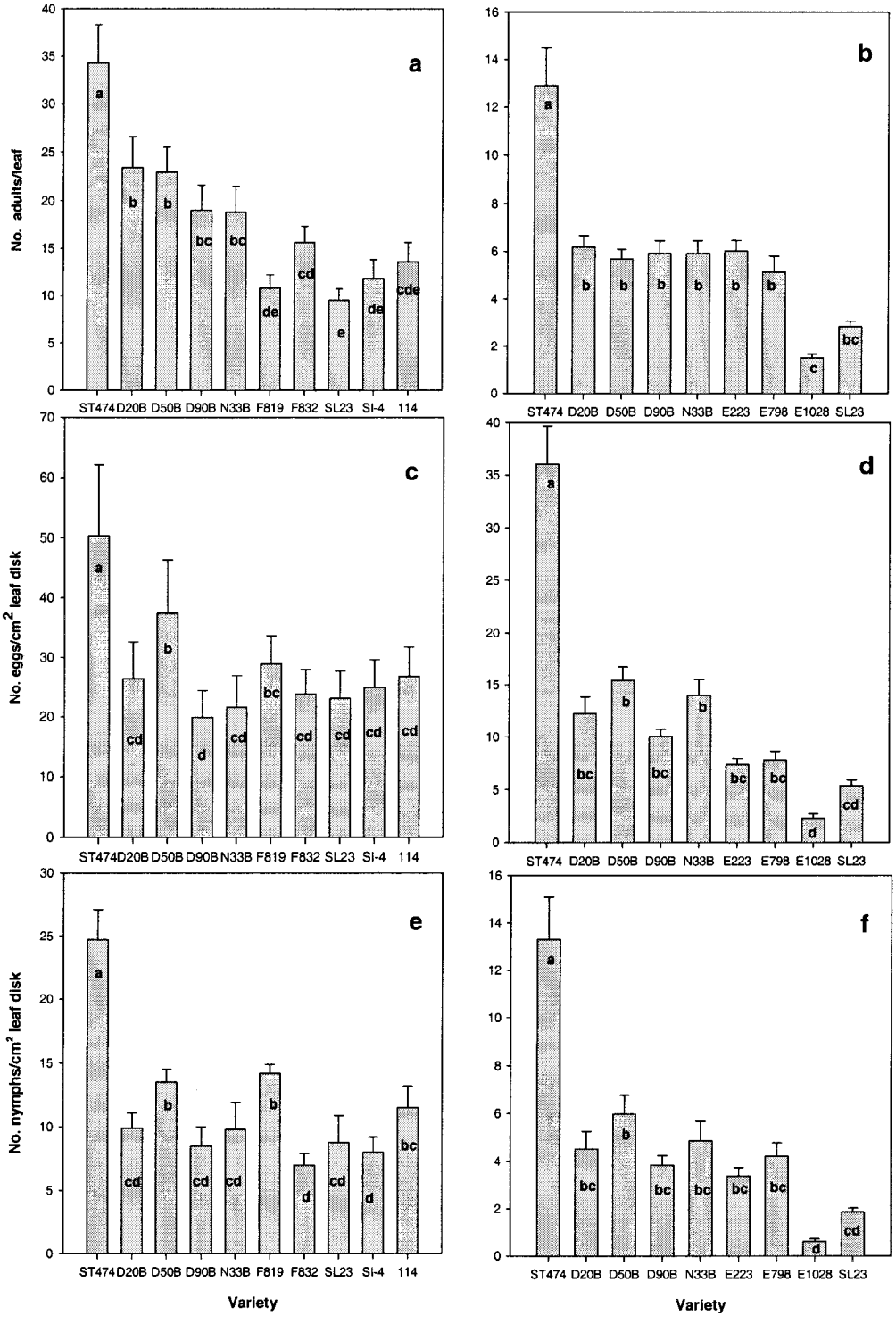

Fig. 4. Seasonal mean numbers of *Bemisia tabaci* biotype B: (a) adults, (c) eggs, and (e) nymphs in 1999 and (b) adults, (d) eggs, and (f) nymphs in 2000. ST, D, N, F, and S are Stoneville, Deltapine, NuCOTN, Fiber Max, and Siokra, respectively. SL23, SI-4 and 8–114 are Siokra L-23, Siokra I-4/649 and 89013–114, respectively. Means of cultivars not followed by the same letters are significantly different (Student-Neuman-Keul's multiple range test, $P = 0.05$). F values were 5.4, 4.0 and 8.1 with df = 9, 27 for 1999 and 13.7, 17.8 and 21.5 with df = 8, 24 for 2000, for adults, eggs and nymphs, respectively.

Table 1. Mean ± SEM numbers of stellate trichomes, *Bemisia tabaci* biotype B eggs and nymphs on leaf disks from leaves for all sampled nodes of ten and nine cotton cultivars, respectively, in 1999 and 2000 at Maricopa, AZ

Leaf node	No./cm^2 leaf disk		
	Stellate tricomes on[a] veins and between veins	Eggs	Nymphs
	1999		
1	199.0 ± 34.3a	22.6 ± 2.0c	0.6 ± 0.1e
3	38.5 ± 6.6b	80.9 ± 7.6a	13.6 ± 1.4b
5	23.0 ± 3.8c	38.0 ± 4.6b	25.6 ± 3.0a
7	13.1 ± 2.8d	17.0 ± 2.1d	16.9 ± 2.3b
10	4.7 ± 1.0e	8.4 ± 0.9e	8.3 ± 0.6c
15	—	3.0 ± 0.3f	4.7 ± 0.2d
	2000		
1	15.0 ± 6.7a	7.8 ± 0.6c	0.8 ± 0.1e
2	10.5 ± 4.9b	12.4 ± 1.7b	2.3 ± 0.3d
3	7.8 ± 3.7c	15.2 ± 2.5a	5.0 ± 0.8c
4	6.3 ± 3.0d	15.6 ± 2.6a	6.6 ± 1.0b
5	5.4 ± 2.6e	13.9 ± 2.2ab	7.6 ± 1.1a
7	3.9 ± 1.9f	8.9 ± 1.3c	6.1 ± 0.8b

Means of in a column not followed by the same letters are significantly different (Student-Neuman-Keul's MRT, $P = 0.05$). F ranged from 11.9 to 250.5 and from 11.4 to 55.1 for 1999 and 2000, respectively, with df = 4, 12 or 5, 15.

[a] On all and small veins, respectively, for 1999 and 2000.

on leaf disks from other nodes. In 2000, the seasonal average numbers of eggs and nymphs for all nine cultivars were the highest on leaves from nodes 3 and 4 for eggs and 5 for nymphs compared with other nodes (Table 1). The seasonal average of trichomes (on small veins and between veins) of all nine cultivars was the highest on leaves from node 1 (15.0 trichomes/cm^2 leaf disk) compared with those on leaf disks from other nodes (Table 2).

Laboratory Studies. Average leaf areas from all leaf nodes of ST 474 and Nu 33B were not significantly different (Table 2). ST 474 had six times as many stellate trichomes on the leaf veins and between veins compared with Nu 33B. Differences in the numbers of capitate trichomes and eggs were not significant between cultivars, but ST 474 had twice as many nymphs compared with Nu 33B. For the two cultivars, the smallest average leaf areas were for leaves from node 1. Leaf areas increased for leaves from nodes 2 to 15. The average numbers of stellate and capitate trichomes were highest on leaves from node 1 and decreased on leaves from nodes 2–15 of both cultivars.

Significantly fewer eggs occurred on leaves from node 1 compared with leaves from nodes 2–5. Numbers of eggs decreased on leaves from nodes 7–10. The mean number of nymphs on leaves from node 1 were significantly less compared with leaves from other nodes. Mean numbers of nymphs on leaves from nodes 3–7 were higher compared with nodes 2, 10, and 15. The regression for mean numbers of stellate and capitate trichomes on leaves from nodes 1–15 were significant ($r^2 = 0.83$, $P = 0.001$, $n = 8$), but regressions of trichome types and egg or nymph densities were not significant (r^2 from −0.01–0.33 or less, P from 0.13 to 0.82, $n = 8$).

Table 2. Mean ± SEM numbers of *Bemisia tabaci* biotype B eggs, nymphs, leaf area, and trichomes on Stoneville (ST) 474 and NuCOTN (Nu) 33B cottons, Maricopa, AZ, 1999

Variable	No./cm^2 leaf disk				Leaf area, cm^2
	Trichomes		Eggs	Nymphs	
	Stellate	Capitate			
	Cultivar				
ST 474	122 ± 14a	1,159 ± 142a	138 ± 27a	46 ± 11a	64 ± 7a
Nu 33B	20 ± 4b	1,506 ± 188a	152 ± 30a	22 ± 4b	67 ± 7a
	Leaf node				
1	146 ± 44a	3,456 ± 376a	123 ± 46bcd	1 ± 0d	22 ± 2f
2	98 ± 25b	1,408 ± 176b	248 ± 65a	22 ± 1bc	39 ± 4e
3	89 ± 28bc	1,215 ± 92bc	228 ± 62ab	68 ± 28a	47 ± 5de
4	70 ± 26bcd	1,187 ± 77bc	254 ± 85a	69 ± 28a	47 ± 4de
5	54 ± 20cd	1,036 ± 119bcd	154 ± 31abc	49 ± 11ab	54 ± 4d
7	35 ± 16d	961 ± 103cd	109 ± 45cd	40 ± 8ab	74 ± 8c
10	42 ± 19d	757 ± 55d	29 ± 5d	14 ± 3bc	93 ± 4b
15	34 ± 15d	642 ± 56d	15 ± 8d	11 ± 3bc	150 ± 7a

Means of cultivars or leaf node in a column not followed by the same letters are significantly different (Student-Neuman-Keul's MRT test, $P = 0.05$). For cultivar comparison, F values were 22.7 and 3.9 for stellate trichome and nymph, respectively, with df = 1, 3. Other parameter comparisons were not significant. For leaf node comparison, F ranged from 3.9 to 74.7 with df = 7, 42.

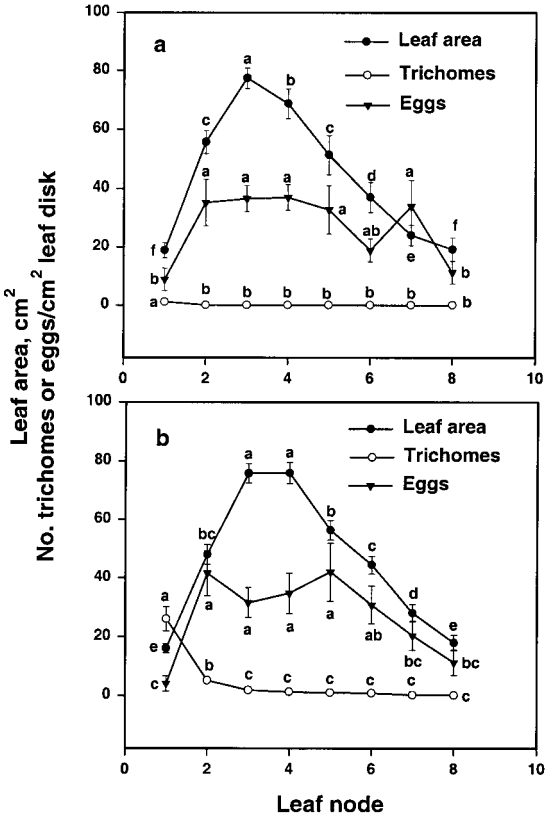

Fig. 5. Mean numbers of *Bemisia tabaci* biotype B eggs, trichomes, and leaf area of leaves from different main stem nodes of greenhouse grown NuCOTN (a) 33B and Stoneville 474 (b). Means within a variable of each cultivar not followed by the same letters are significantly different (Student-Neuman-Keul's MRT test, $P = 0.05$). F values were 23.1, 5.2, 4.8 for NuCOTN 33B and 45.5, 5.3, and 55.2 for Stoneville 474 for leaf area, eggs and trichomes, respectively, with df = 7, 63.

Greenhouse Studies. After exposure of clean plants to equal numbers of adult *B. tabaci* with different leaf ages (from nodes 1 to 8), mean numbers of eggs on Nu 33B leaves from nodes 1 and 8 (8.9 and 11.3 eggs/cm^2 leaf disk) were significantly different compared with leaves from nodes 2–7 (18.9–36.6 eggs/cm^2) (Fig. 5a). Mean numbers of stellate trichomes were significantly higher on Nu 33B leaves from node 1 (1.13 trichomes/cm^2 leaf disk) compared with leaves from other nodes (0.00–0.05 trichomes/cm^2 leaf disk). For ST 474, fewer *B. tabaci* eggs were found on leaves from nodes 1 and 8 (4.1 and 11.3 eggs/cm^2) compared with leaves from nodes 2 to 6 (20.4–42.0 eggs/cm^2 leaf disk) (Fig. 5b). Also, numbers of stellate trichomes on ST 474 leaves were higher on leaves from node 1 (26.08 trichomes/cm^2 leaf disk) compared with leaves from other nodes (0.16–5.20 trichomes/cm^2 leaf disk). ST 474 also had 23 times more stellate tricomes on node 1 leaves compared with Nu 33B. Leaves from nodes 1 and 8 were smaller compared with leaves from 3 to 7.

Discussion

It has been well documented that hairy leaf cotton cultivars are associated with higher *Bemisia* populations compared with smooth leaf cultivars (Mound 1965, Butler and Henneberry 1984, Flint and Parks 1990, Norman and Sparks 1997). Butler et al. (1991) reported that *Bemisia*-trichome (stellate) density was positively related, but adult densities decreased when trichome density become too high and apparently affected *Bemisia* activity. These results appear to agree with Mound (1965), who did not find whitefly adults or eggs on the first two top leaves of some exceptionally hairy cotton plants. Results of our study suggest other factors may also be involved.

Our studies showed the youngest leaves at the top of the plants on both hairy and smooth leaf cultivars always had the highest stellate and capitate trichome densities, but frequently, the least numbers of *B. tabaci* eggs and nymphs (Tables 1 and 2 and Fig. 5a and b). Eggs and nymphs accumulate on leaves over time. Youngest leaves on tops of plants (node 1) in the field when sampled have been exposed to adult oviposition for shorter times compared with older leaves that might bias results for old versus young leaf comparisons. After exposure of different age leaves (nodes 1 to 8) to equal numbers of adult *Bemisia*, the fewest numbers of eggs were laid on the youngest leaves (node 1) (Fig. 5a and b). This appears in contrast to the positive trichome–whitefly density relationships at least for our studies with individual plants. Top young leaves have thinner leaf laminae and yellowish green color compared with thicker and darker green older leaves (Chu et al. 2000a, 2000b). These and other leaf characteristics, such as nutritional value (Byrne and Draeger 1989), may affect *Bemisia* colonization.

The reasons why hairy leaf cultivars harbor higher whitefly populations remains unknown. Leaf hairiness and the associated increased boundary layer humidity on leaf surfaces may be involved (Burrage 1971). Under hot and dry climatic conditions, a subtle change in abaxial leaf surface humidity may affect the survivorship of eggs and nymphs, particularly first instars which have limited energy reserve and are easily dehydrated (Cohen et al. 1998). Earlier reports suggested that leaf hairiness protected whiteflies from predators and parasites (Li et al. 1987, Heinz and Zalom 1995). It has also been suggested that *Bemisia* adults and nymphs use trichomes to locate feeding-reproduction sites (Cohen et al. 1996a, 1996b, 1998).

The development of plant resistance to *Bemisia* infestation remains a viable and highly desirable objective. Leaf hairiness and other morphological characteristics identified to date do not appear to be effective enough to provide acceptable protection from *Bemisia* infestations. Other possible approaches include investigations on the effects on *Bemisia* of secondary products such as terpenoids (e.g., gossypol), tannins and lignins that are produced by cottons. These characteristics developed in combination with leaf hairiness and morphological characteristics may

provide a diversity of biological barriers resulting in plant resistance to cotton pests (Bell 1986).

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